

EARLY PRIMARY SUCCESSION ON DUNES AT BODEGA HEAD, CALIFORNIA

AVINOAM DANIN

Evolution, Ecology, and Systematics, Hebrew University of Jerusalem,
Israel 91904

STEPHEN RAE

MUSCI, 1130 Cayetano Court, Napa, CA 94559
{srae@musci.com}

MICHAEL BARBOUR AND NICOLE JURJAVCIC

Environmental Horticulture, University of California, Davis, CA 95616

PETER CONNORS AND ELEANOR UHLINGER

Bodega Marine Laboratory, Bodega Bay, CA 94923

ABSTRACT

Field examination of dune hillocks (nebkas) showed that changes in nebka topography and spread, sand texture, vascular plant and cryptogam cover, and species presence were correlated with nebka ages between 15 and 135 yr. We determined age by a series of aerial photographs dating back to 1955 and topographic maps drawn as early as 1862. Development of a cryptogamic crust was significant during this range of time; on the oldest nebka it contributed 43 g biomass m⁻² of nebka surface, which represented 3% of total above-ground biomass. Nebkas at Bodega grew in height 4 cm yr⁻¹ during the past century, whereas non-vegetated areas were deflated at the same rate. Succession is driven by sand-stilling attributes of *Ammophila arenaria*, introduced to northern California in the mid-nineteenth century and additionally planted at Bodega in the mid-twentieth century. By reference to the 1862 map we concluded that *A. arenaria* has built a prominent, continuous foredune and hinddune since the time of its arrival.

Some of the earliest American concepts about succession came from studies of coastal dunes (Cowles 1901), and the Pacific coast dunes were one of the first Californian ecosystems to be monographed (Cooper 1936, 1967). Despite this history, most published information about primary succession on California dunes is largely anecdotal and inferential (Barbour and Johnson 1988; McBride and Stone 1976; Barbour et al. 1981; Holton and Johnson 1979).

California dunes have been invaded in this century by *Ammophila arenaria* (L.) Link (European beachgrass) to the point that the prior dominant, *Leymus mollis* (Trin.) Pilger ssp. *mollis* (American dunegrass), has been virtually eliminated from many dune locations, with consequent changes in dune topography, species richness, and (probably) primary succession. Furthermore, no attention has been paid to the role of cryptogams in California dune succession, even though the broad importance of biological crusts to ecosystems with sand substrates is well known (e.g., Danin 1996; Dor and Danin 1996; St. Clair and Johansen 1993).

Our objective was to begin a study of dune succession, with a focus on changes in dune topography, sand texture, vegetation cover, species richness, and growth forms.

MATERIALS AND METHODS

Study area. Our study location is the Bodega Marine Reserve (Fig. 1), property managed by the University of California for the purpose of biological research and teaching. The physical and biological setting of Bodega Head have been described in detail by Barbour et al. (1973), Koonig (1963), Light et al. (1967), Lipps and Moores (1971), Standing et al. (1975), and Diamond and Kennedy (1975).

The reserve consists of 132 ha in the middle of Bodega Head Peninsula, located approximately 80 km north of San Francisco at 38°19'N latitude and 123°04'W longitude. The rocky, granitic headland is abruptly truncated within the Reserve's boundaries by the San Andreas Fault. Northeast of the fault is a 0.7–1.7 km by 3.5 km swath of relatively open dunes jointly administered by the University of California and the California Department of Parks and Recreation. Climate type is maritime-moderated-mediterranean. Annual precipitation is 78 cm, about 80% of which falls in the months November through March. Daily and seasonal amplitudes of temperature are modest and frosts are rare. Mean annual air and surface water temperatures are both 12°C. The majority of summer days have morning and evening fog. Prevailing winds are from the northwest and average 15 kph; spring

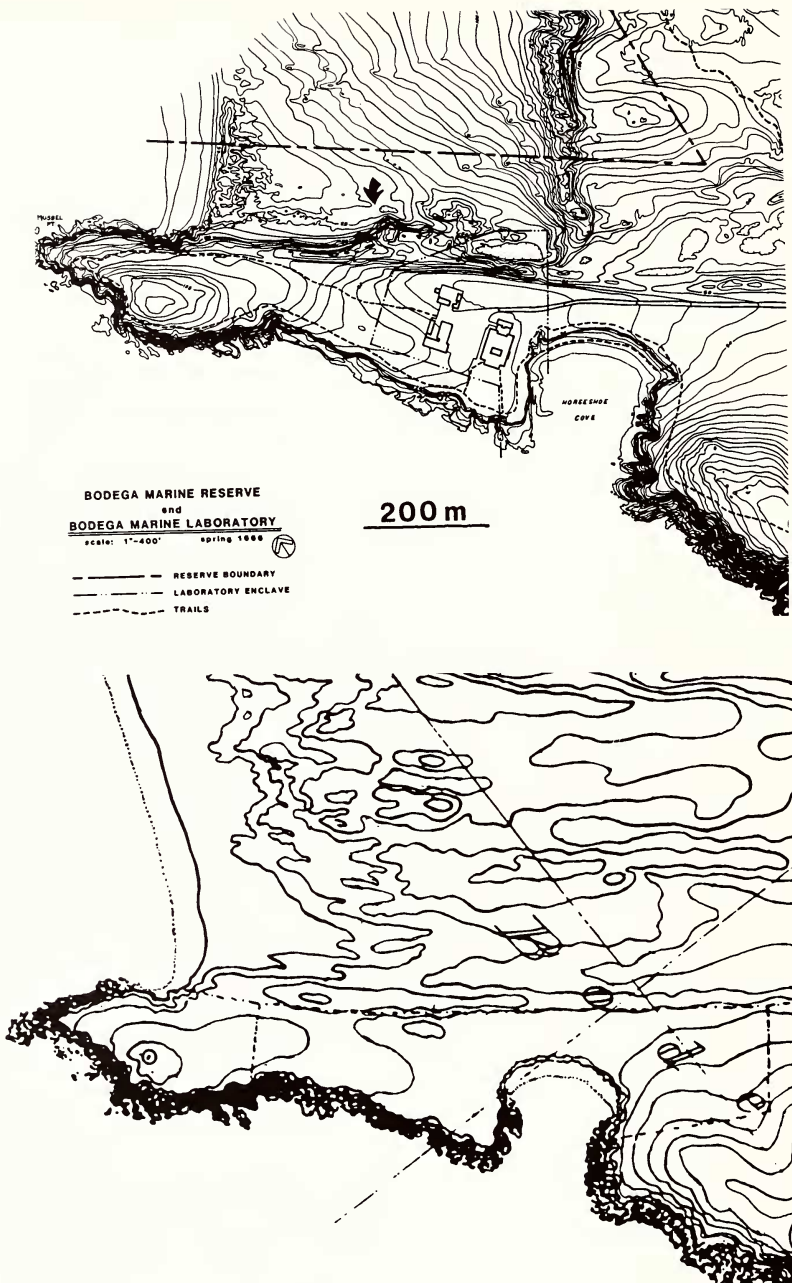


FIG. 1. Paired contour maps of a portion of Bodega dunes. The 1986 map (top) has 5 ft contours; the 1862 map (bottom) has 20 ft contours. The intersection of lines on the 1862 map, just above (north of) Horseshoe Cove, corresponds to 38°19'N latitude × 123°03'W longitude. The approximate location of our 30 × 150 m study plot is shown by the arrow (top). Scale for both maps is shown on the 1986 map.

is the windiest season, with afternoon northwest winds averaging 30–50 kph on many days. Dune sand originates as material eroded from northern watersheds and carried south by ocean currents.

Bodega Head and the adjacent dunes were occupied by Coast Miwok for at least the past 3000 yr, judging from well-documented artifacts includ-

ing shell middens (Colley 1970; Greengo 1951). Russian settlers established a farming settlement early in the nineteenth century, but retreated to Alaska in the 1840's. American settlers since that time have used the area mainly for dairy cattle grazing, farming, and sheep pasture. It is probable that dune plant cover declined as a result of grazing

and farming, and that the dunes became more mobile than they were during Indian occupation. Sand encroachment into Bodega Harbor this century has required periodic dredging to keep shipping lanes open. Between the 1920's and 1950's, extensive portions of the dunes were planted to European beachgrass in an attempt to stabilize the sand and minimize the need for repeated dredging.

Now, the dunes are a mosaic of densely vegetated areas, barren blowouts, swales, and scattered hillocks which have some degree of vegetative cover. We will hereafter call hillocks "nebkas," a north-African term meaning a topographic feature created by the sand-stilling nature of vegetation rooted in sandy substrate. Our focus is on a relatively open, 500-m-deep region, between a 5 m tall foredune and a 45 m tall hinddune. The foredune and hinddune vegetation cover is dominated by *A. arenaria* and the shrub *Lupinus arboreus* Sims (bush lupine, a California native here near its natural northern limit; Davidson and Barbour 1977). Aerial photographs and historical information both confirm that this study area was not included in the *A. arenaria* plantings of this century.

An 1862 topographic map of the dune area (Fig. 1; Rodgers and Kerr 1862; original scale 1:10,000), compiled before any *A. arenaria* was present, shows neither a foredune nor a hinddune, and instead details a series of low, broken dune ridges running perpendicular to the coast. Evidently, Bodega dune topography has been modified by the past century's displacement of native vegetation by *A. arenaria* in much the same way Cooper (1967) concluded *A. arenaria* had changed other parts of the Pacific coast.

Field sampling methods. Our intention was to select a series of adjacent nebkas of varying age. Using a series of aerial photographs of the dunes taken in 1955, 1971, 1977, 1988, 1990, and 1991, we identified four adjacent nebkas (Fig. 2A–D) that appeared at different times. These four occurred in a 30×150 m rectangular area with long dimension perpendicular to the shore, parallel to prevailing winds and remnants of nineteenth century dune ridges. Prevailing wind direction is from nebkas A to nebkas D. Nebka D is the windward portion of a ridge, hence differs in its present form from the island-like nebkas A, B, and C.

In the late spring of 1995, we mapped each nebkas's edges to scale. The edge was identified by a congruence of: significant change in slope, plant cover, and surface coarseness. The high point of each nebkas was marked with a pole and transect tapes were laid out in the four cardinal compass directions (N, E, S, W). We measured transect lengths to nebkas edges. Using an inclinometer, we calculated nebkas height relative to the edge. We sampled plant and cryptogamic cover by taking a point sample along north and east transects, the directions typically with highest plant cover due to

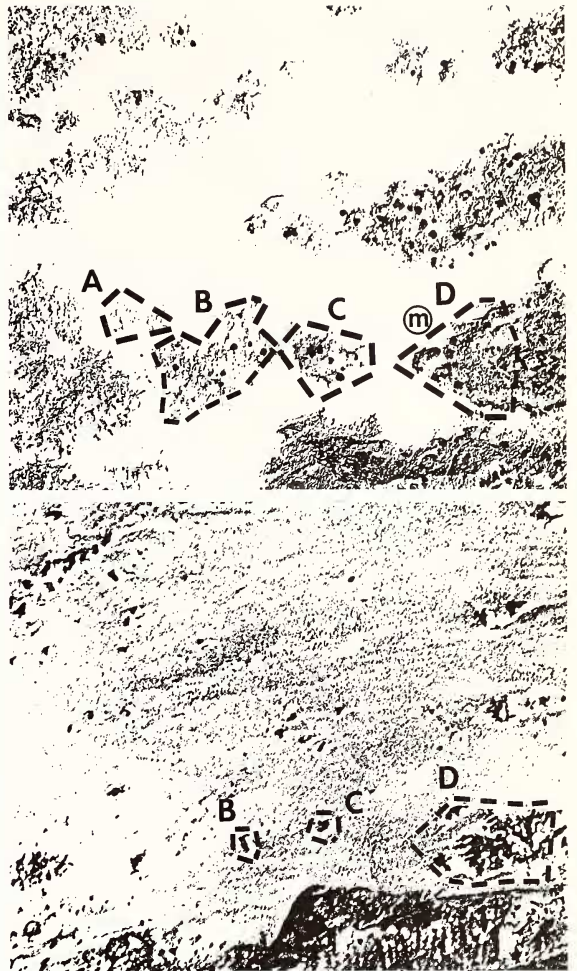


FIG. 2. Paired aerial photographs of our study plot taken in 1991 (top) and 1955 (bottom). The 1991 photograph shows nebkas A–D and an exposed midden (m), whereas the 1955 photograph shows only nebkas B–D. The shore (west) lies to the left, just out of view. The area of nebkas A–D is approximately 30×150 m.

aspect or protection from prevailing winds. If no species covered a point the point was recorded as bare, and total percent cover was calculated as the percent of points with vegetation.

Cryptogams were sent to experts for determination: mosses to Bruce Allen, Marshall Crosby, and Alan Whittemore of the Missouri Botanical Garden, and to Dan Norris of the University of California, Berkeley; and lichens to Clayton Newberry of the University of California, Berkeley. Reference specimens are deposited in those herbaria. Determined vascular plant taxa and specimens are deposited in both the University of California, Davis and the Bodega Marine Laboratory herbaria. Vascular plant nomenclature follows Hickman (1993).

We collected sand samples of 500–1000 g size at two depths and nine locations for each nebkas: from the surface 2 cm and the subsurface 10–12

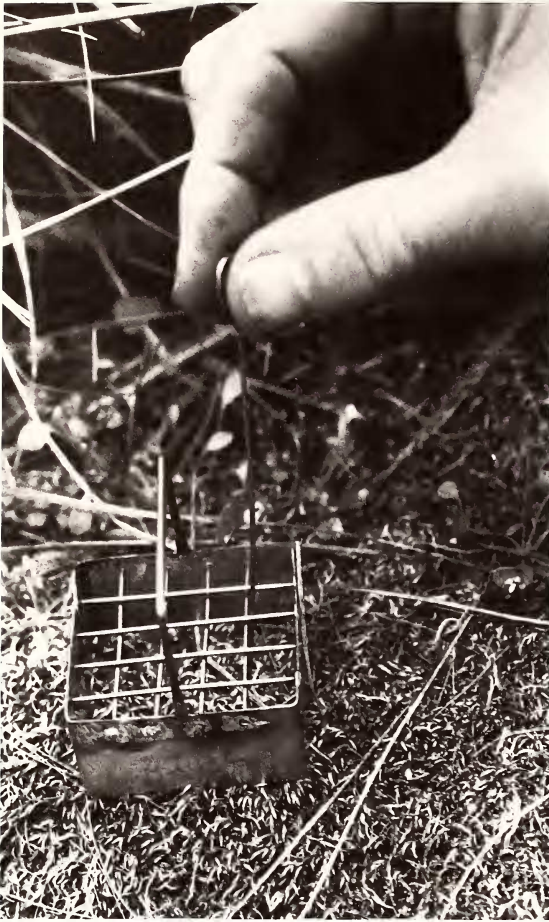


FIG. 3. Metal frame device used to extract plugs of cryptogamic crust 2 cm thick and 5×5 cm in area.

cm at the nebka center, midway along each of the four transects, and at the end of each transect. An equal number of random samples were collected from internebka locations. Samples were oven-dried at 105°C for 48 hr, then shaken on a reciprocating shaker for 3 min through a sequence of standard sieves: 2.0, 0.5, 0.25, and 0.05 mm. These sizes separated five fractions as: gravel, coarse sand, medium sand, very fine sand, and silt + clay, respectively (Gee and Bauder 1986; USDA 1951).

We also sampled the biotic crust for organic matter content and sand texture. We constructed a metal sampling device (Fig. 3) to extract a plug of crust

5×5 cm square and 2 cm deep. The top 3–4 mm of the plug consisted of green moss or lichen matter, whereas the rest consisted of living, pale-to-nongreen moss material. The top of the device was criss-crossed with fine wires, giving 16 intersections which could be used as points for making cover estimates. We chose sample locations subjectively to provide single-species samples of crusts dominated by the most abundant cryptogams: the fruticose lichens *Cladonia fimbriata* (L.) Fr. and *C. macilenta* Hoffm. and the mosses *Brachythecium albicans* (Hedw.) BSG and *Didymodon vinealis* (Brid.) Zander. The only other cryptogam in the study site, the moss *Bryum capillare* Hedw., was restricted to a single nebka and therefore we did not sample its biomass. We also required that sampled crusts be exclusively comprised of one taxon only and that it covered 100% of a minimum area of 6×6 cm. We extracted three samples of each species of crust from each of three nebkas.

The samples were oven-dried at 105°C for 48 hr, at which time they ranged in weight between 50 and 140 g. Organic matter was chemically determined by potassium dichromate reduction and spectrophotometric measurement (a modified Wilkley-Black method; Nelson and Sommers 1982) and the samples were sieved to determine sand texture.

We measured changes in areas of nebkas A–D over time by examining sequential aerial photographs. We projected photographs onto a screen, traced nebka boundaries on graph paper, measured virtual areas, and converted them to actual areas by reference to the photograph's scale. We estimated our range of error to be $<10\%$.

RESULTS

Nebka size, topography, and age. Present nebka height increased from <1 m for nebka A to >4 m for nebka D (Table 1). Present nebka area in general increased from A to D, although nebka B was larger than nebka C. Recall that nebka D was on the windward end of an old, elongate ridge; we arbitrarily defined the sample area as the most northwestern 4000 m^2 portion. Nebka area thus differed at the A and D extremes by an order of magnitude.

In 1955, nebkas B, C, and D were present, but B and C were very small ($30\text{--}40 \text{ m}^2$ each), two orders of magnitude smaller than at present (Table 2 and Fig. 2). We estimate that the year of origin

TABLE 1. PHYSICAL TRAITS OF NEBKAS A, B, C, AND D, AS OF SPRING, 1995. Within a row, numbers with different superscript letters are statistically different at $P < 0.5$.

Trait	A	B	C	D
Area (m^2)	378	1256	908	4000
Height (m)	0.4	2.0	2.9	4.6
Coarse sand (%)	34.1 ^a	28.3 ^b	23.3 ^b	10.8 ^c
Very fine sand (%)	6.8 ^a	10.0 ^b	10.3 ^b	12.7 ^b

TABLE 2. APPROXIMATE AREA (m²) OF EACH NEBKA AND OF A NEARBY MIDDEN OVER TIME. Based on interpretation of aerial photographs for all years prior to 1995, and on-the-ground-measurements in 1995. Nebka D, which remained constant at >4000 m², is not shown.

Year	Nebka A	Nebka B	Nebka C	Midden
1955	0	30	40	0
1971	0	160	115	100
1977	0	240	110	80
1988	290	1410	515	180
1990	470	2090	840	305
1991	440	2120	1120	375
1995	380	2205	910	400

for B and C did not long precede the 1955 photograph, and certainly was not equal to that of well-developed nebka D. Provisionally, we assigned an age of 45 yr to nebkas B and C. Nebka D—that is, the ridge to which it is the windward front—appears to have been present in the 1862 topographic map. Provisionally, we assigned an age of 135 yr to nebka D.

Nebka A did not appear until the 1988 photograph, at which time it measured nearly 300 m² in

area. We interpret this relatively large size as indicating that its year of origin was closer to 1977 than to 1988. Provisionally, we assigned an age of 15 yr to nebka A. The present star-shaped appearance of nebka A may indicate that it was created by a single establishment event; that is, the star's rays are the results of *A. arenaria* rhizomatous spread from the single establishment locale.

The rate of growth in nebka area was unequal among the four nebkas (Table 2). It was essentially zero for nebka D. Nebkas A, B, and C grew in geometric fashion, slowly at first and then more rapidly over time. Within intervals, however, growth rates differed, nebkas A and C typically growing more slowly than nebka B (Table 2). Nebka B has increased in area 70-fold since 1955, whereas nebka C has increased only 25-fold. The current height of B, however, is nearly 1 m lower than that of C, thus aerial and vertical accretion seem to be uncoupled in this system. Growth for all three nebkas was slow in 1991–1995 compared to earlier periods of time.

Vegetative cover and richness of species and growth forms differed appreciably among the four nebkas (Table 3). Nebka A, the presumed pioneer

TABLE 3. VEGETATIVE COVER, IN 1995, ON THE FOUR NEBKAS. Data, in percent, are averages of two line transects, with point data taken every 50 cm. T = <0.1%; — = not present.

Growth form and species	Nebka A	Nebka B	Nebka C	Nebka D
Shrubs				
<i>Lupinus arboreus</i>	—	11.6	22.1	10.3
<i>Baccharis pilularis</i>	—	—	7.8	5.2
Herbs				
<i>Ammophila arenaria</i>	40.1	67.7	41.8	90.9
<i>Cardamine oligosperma</i>	4.9	5.7	5.2	10.8
<i>Claytonia perfoliata</i>	3.7	9.1	1.9	15.2
<i>Lotus heermannii</i>	2.4	—	—	—
<i>Camissonia cheiranthifolia</i>	T	0.7	1.4	—
<i>Carpobrotus chilensis</i>	T	—	—	—
<i>Conyza canadensis</i>	T	—	T	—
<i>Brassica rapa</i>	—	0.9	—	—
<i>Gnaphalium purpureum</i>	—	1.7	—	—
<i>Ambrosia chamissonis</i>	—	0.9	—	—
<i>Crassula connata</i>	—	3.0	1.9	—
<i>Spergularia macrotheca</i>	—	0.9	7.7	—
<i>Erechtites minima</i>	—	0.7	T	1.1
<i>Carpobrotus edulis</i>	—	—	4.1	—
<i>Daucus pusillus</i>	—	—	T	T
<i>Juncus bufonius</i>	—	T	—	—
<i>Galium aparine</i>	—	—	—	T
<i>Poa douglasii</i>	—	T	—	—
<i>Solanum americanum</i>	—	—	T	—
Cryptogams				
<i>Bryum capillare</i>	—	—	—	0.8
<i>Didymodon vinealis</i>	T	4.7	T	0.8
<i>Brachythecium albicans</i>	T	0.9	7.1	10.5
<i>Cladonia fimbriata</i> and <i>C. macilenta</i>	T	T	—	—
Total number of species	10	16	15	11
Bare ground (%)	49.0	17.9	25.3	8.2
Number of samples	61	135	63	115

TABLE 4. ORGANIC MATTER IN THE TOP 2 cm OF BIOTIC CRUST. Data are means of three samples, one sample per nebka. Within a column, data with a different superscript statistically differ at $P < 0.5$.

Dominant cryptogam	OM as %	OM as g m ⁻²
<i>Cladonia</i> spp.	30.3 ^a	497 ^b
<i>Brachythecium albicans</i>	29.6 ^a	408 ^b
<i>Didymodon vinealis</i>	31.9 ^a	269 ^c

phase, had the fewest species and the lowest vascular plant and cryptogamic cover. Nebka A lacked the presence of shrub taxa. Nebkas B and C had the most species and an intermediate amount of plant cover. Nebka D had almost as few taxa as nebka A, yet exhibited the most plant and cryptogamic cover.

The contribution of cryptogams to plant cover increased from trace, to 5.6, to 7.1, and to 11.3% on nebkas A–D, respectively. Cryptogamic cover was typically patchy, covering the entire surface in local 0.2–0.5 m² areas, while virtually absent elsewhere. The organic matter content of the topmost 2 cm in such patches averaged 30% by weight, or 391 g m⁻² crust. There was significantly less biomass per unit area for the moss *D. vinealis* among the three cryptogams sampled (Table 4), but the other taxa were not statistically different from each other.

From Table 3, we can estimate that 11% of a mature nebka's surface would contain a biotic crust such as we sampled, and therefore the standing biomass would be ($0.11 \times 391 = 43$ g m⁻²).

Sand texture differed among nebkas, coarse sand (2.0–0.5 mm) and very fine sand (0.25–0.05 mm) fractions showing the most difference. Gravel (>2 mm) and silt + clay (<0.05 mm) fractions combined never accounted for >1% of any sample's weight. Surface and subsurface textures, however, were not statistically different, hence we have pooled those data in this paper. Textures at the nebka center and midway along the transects were insignificantly different among the nebkas, but they were different from texture at the nebka edge. Consequently, each nebka's texture data in this paper represent average data for ten samples: surface and subsurface samples at the nebka's center and midway along each of its four transects. Nebka sand

texture was significantly finer than sand at nebka edges or at random internebka locations (Table 5).

One layer of coarse sand, approximately 2 m below the current surface of several ridges and of nebka D, was uniquely coarsest of all samples. We think this stratum was the result of a period of intense erosion during which finer particles were blown away. Our examination of the series of aerial photographs lead us to conclude that this coarse layer was at the surface just after 1955. One reason for our choice of 1955 was the presence of a midden mound adjacent to nebka D (Fig. 2 and Table 2) in the 1971 photograph, but not visible in the 1955 photograph. By 1995, the midden's exposed area had quadrupled from that in 1971, indicating that scouring of the unvegetated surface is continuing. The location of the coarse sand layer today, 2 m below the vegetated surfaces of ridges and nebka D, indicates an average sand accretion rate of 5 cm per year. This rate of accretion is modest compared to known rates for *A. arenaria* dunes elsewhere that approach 100 cm per yr (Barbour et al. 1985). At the same time, there must have been an equal amount of deflation between the ridges because the height of the coarse stratum is about 2 m above present internebka swales.

DISCUSSION AND CONCLUSIONS

The vegetation on nebkas A–D fits within the definition of dune scrub dominated by *A. arenaria* formally classified as "European beachgrass" series by Sawyer and Keeler-Wolf (1995) or as "*Ammophila-Erechtites*" and "*Ammophila-Baccharis*" communities by Parker (1974).

Ammophila arenaria today has a central importance to nebka formation, vegetation succession, and the composition of dune scrub on stabilized substrates at Bodega Head. We can presume that modern dune succession and dune scrub differ from that of the last century (when *Leymus mollis* was the dominant sand-stilling grass) because published studies show that *A. arenaria* grows more densely than *L. mollis* and that it suppresses species richness and cover from other taxa (Barbour and Johnson 1988; Barbour et al. 1976; Pavlik 1983).

Remnant areas of northern California dune scrub still dominated by *L. mollis* exist at Point Reyes National Seashore, Lanphere-Christensen Dunes

TABLE 5. SOIL TEXTURE. Coarse = a buried stratum found repeatedly beneath several nebkas and dune ridges. Internebka data come from five random samples within the 50 × 150 m study area. Edge = the surface and subsurface samples combined from 16 samples at nebka outer edges. Within = the surface and subsurface samples combined from 20 samples taken within nebkas. Data to the far right represent soil texture just beneath biotic crusts of *Cladonia*, *Brachythecium*, and *Didymodon*. Within a row, numbers with different superscripts are statistically different at $P < 0.5$.

Texture class	Coarse	Internebka	Edge	Within	Clad	Brach	Didy
Coarse sand	73.8 ^a	53.1 ^a	38.8 ^a	22.1 ^b	18.4 ^b	9.0 ^c	7.3 ^c
Very fine sand	7.7 ^d	11.7 ^d	8.9 ^d	10.0 ^d	15.3 ^c	21.4 ^c	26.3 ^c
No. samples	2	5	32	40	3	3	3

Preserve, just south of the mouth of Ten Mile River in Mendocino County, and in very local patches along Bodega Bay. This vegetation has been variously described as "native dunegrass," "yellow bush lupine," and "coyote brush" series by Sawyer and Keeler-Wolf (1995), as "*Baccharis-Scrophularia*," "*Poa-Lathyrus*," and "*Solidago spathulata-Lupinus* arboreus dune mat" communities by Parker (1974), or as "*Lupinus arboreus-Haplopappus ericoides*" association by Holton and Johnson (1979).

Vegetation on nebkas A–D are related by patterns commonly reported for progressive succession in general (Barbour et al. 1987). For example, total cover increases through the entire sere, but species richness peaks at an intermediate phase. We presume that the late-seral decline in species richness is due to growing dominance by *A. arenaria* and its homogenization of the microenvironment, reducing niche diversity.

The few studies of plant zonation and putative succession on California dunes suggest that the most highly correlated abiotic factors (possible drivers of succession) are: coarseness of the substrate, amount of soil organic matter, wind speed near the surface, intensity of salt spray, and degree of surface sand movement (Barbour 1992; Barbour et al. 1973; Barbour and DeJong 1977; Barbour 1978; Holton and Johnson 1979; Johnson 1963; McBride and Stone 1976; Parker 1974).

Our results corroborate and add detail to the published pattern of increasingly fine sand texture accompanying the progression of primary succession. The percent of coarse sand monotonically declined nearly an order of magnitude from internebka sand to sand at the edge of nebkas, to sand well within nebkas, and to sand within a cryptogamic crust on nebkas. At the same time, the percent of very fine sand more than doubled. Although we collected no data on the ecological effect of this textural cline, we can easily imagine that increasingly fine texture improves soil moisture retention. We can also infer that the driving factor for increasingly fine texture is declining surface wind speed, which allows smaller particles to settle out (Danin and Yaalon 1982; Danin 1996). Thus, gradients of sand movement, salt spray, and wind speed are all undoubtedly interdependent in this ecosystem.

Our observation of a widely distributed layer of exceptionally coarse sand gave us a possible datum from which to estimate rate of nebka building or internebka deflation. The 15-cm thick layer (Table 5; Fig. 4) had 39% more coarse sand and 34% less very fine sand than average internebka samples. It was visible at a consistent depth of about 2.0 m beneath stabilized ridges or large nebkas, and at a similar height above internebka swales and blow-outs. The coarse layer may represent surface material prevalent prior to the widespread planting of *A. arenaria* and the creation of a foredune which has since slowed surface winds. It could have been

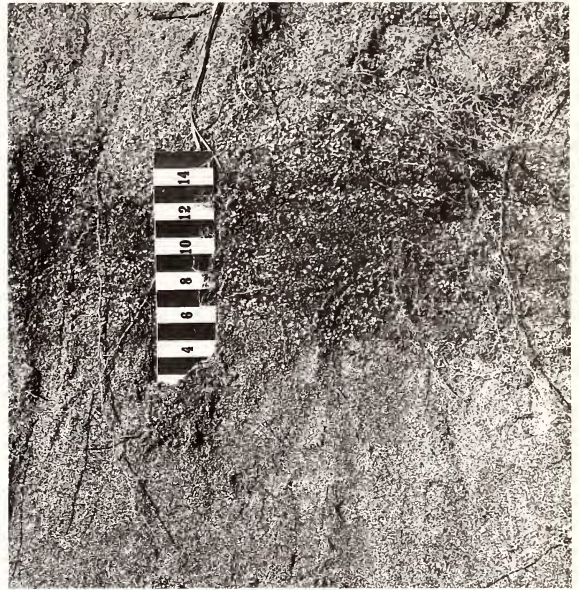


FIG. 4. Stratum of visibly coarse sand about 2 m below the current vegetated surface of ridges and mature nebkas.

present on the surface as recently as 1955 based on our interpretation of aerial photographs. If so, this burial has been the result of sand-stilling vegetation, trapping 2 m of sand in a span of 40 yr (average annual rate of accumulation = 5 cm). We know that short-term sand accumulation rates driven by the presence of *A. arenaria* may approach 1 m yr⁻¹ along the foredune (Barbour and Johnson 1988; Barbour et al. 1985), but there are no published records of long-term sand accumulation rates in the lee of the foredune with which we can compare our deduced rate of 5 cm yr⁻¹.

Our study has shown that the role of cryptogams in nebka formation and vegetative biomass accumulation is significant. The percent cover of a cryptogamic crust increased monotonically with presumed nebka age and physical complexity. On the presumed oldest nebka D, the 2-cm-thick crust contained an average of 391 g organic matter (biomass) per square meter of crust, or 47 g m⁻² of nebka surface. This is not a trivial contribution to above-ground biomass. According to a more extensive California coast study by Barbour and Robichaux (1976) vegetation dominated by *A. arenaria* has a biomass of 1819 g m⁻² dune surface when its cover is 100%. Nebka D had 91% cover by *A. arenaria*; ignoring any other plant cover, this would translate as (0.91 × 1819) 1655 g m⁻² nebka surface. Thus, the cryptogamic biomass, 47 g m⁻², is 3% of total above-ground biomass. We expect that the contribution of biotic crust to biomass is even higher beyond the hinddune, where older and more stabilized dunes have a more continuous crust. However, there are no data yet collected for that part of the Bodega dunes ecosystem.

We have also been able to conclude that a continuous hinddune and foredune did not exist at Bodega Head prior to the introduction of *A. arenaria*. An 1862 survey map shows a gradual increase in base sand surface to the east and inland from tideline, reaching about 25 m elevation and—superimposed on this basal surface—a series of broken ridges running perpendicular to shore with maximum heights of 40 m. The distribution of peak ridge heights resembled a string of islands roughly parallel to shore and situated about 470–500 m inland. These peaks were approximately 100–150 m more shoreward of today's 45-m-tall hinddune that lies 600–650 m inland. The development of the hinddune was already substantially complete by 1958 according to a map prepared by Pacific Gas and Electric Company (PGE 1958), only a decade after wide-spread planting of *A. arenaria*. The impact of *Ammophila* on foredune topography thus matches that described recently for the northwest coast of North America in general by Wiedemann and Pickart (1996).

Finally, the rate of spread of *A. arenaria* on Bodega nebkas paralleled a pattern reported for more extensive dunes near Arcata, CA over the period 1939–1989 (Buell et al. 1995). In that study, *A. arenaria* first spread slowly, then entered a phase where the square root of area was linearly related to time in years. Bodega nebkas B and C (Table 2) showed a similar slow phase of increasing area between 1955 and 1971, then a linear increase phase thereafter. The linear phase exhibited an average increase of 100 m² yr⁻¹ per nebkas.

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